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ORIGINAL ARTICLE

An experimental approach to the formation of diet preferences and individual specialisation in European mink

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Abstract Individual dietary specialisation can occur within populations even when average diets suggest that the population has a generalist feeding strategy. Individual specialisation may impact fitness and has been related to demographic traits, ecological opportunity, competition, learning and animal personality. However, the causation and formation of individual specialisation are not fully understood. Experiments on animals raised in controlled environments provide an opportunity to examine dietary preferences and learning largely independent from variation in lifetime experiences and ecological opportunity. Here, we use a feeding experiment to examine individual specialisation and learning in captive bred European mink (*Mustela lutreola*) in an Estonian conservation programme. In a series of cafeteria experiments, animals could choose between one familiar food item (Baltic herring *Clupea harengus membras*) and two initially novel ones (noble crayfish *Astacus astacus* and house mouse *Mus musculus*). In general, mice were rarely eaten whilst crayfish consumption increased over time and fish decreased. At the individual level, there was a mix of generalists and crayfish or fish specialists, and the individuals differed in learning time in relation to novel prey. Our results indicate that individual variation in innate preferences and learning both contributes to individual diet specialisation. The differences in learning indicate individual variation in behavioural plasticity, which in turn can be related to personality. This could be of concern in conservation, as personality has been shown to affect survival in translocations.

Keywords Diet · Individual specialisation · Learning · Conservation · Translocation · *Mustela lutreola*

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Introduction

The average diet in generalist populations may not reflect the actual ecology and behaviour of individuals, as individual specialisation can occur (Araujo et al. 2011). In vertebrates, individual specialisation can be related to characteristics such as sex (e.g. Clutton-Brock 2007), age group (Polis 1984) and morphology (Snowberg et al. 2015), but it may also be independent of these factors (Bolnick et al. 2003; Tinker et al. 2008). In these cases, individual specialisation has been suggested to depend on both genetic and environmental characteristics (Araujo et al. 2011). Individual specialisation may also be plastic in response to changing conditions (Svanbäck and Bolnick 2007; Knudsen et al. 2007; Bolnick et al. 2010). A number of environmental cues have been linked to individual specialisation and niche breadth, both on individual and population levels, including density dependence (Tinker et al. 2012), prey abundance (Tinker et al. 2008), predation and inter- or intraspecific competition (Svanbäck and Bolnick 2007; Knudsen et al. 2007; Bolnick et al. 2010). However, the formation of feeding strategies is also likely to be affected by social learning and experience in handling different prey types (Huffman and Quiatt 1986; Lefebvre 1995; Terkel 1996; Tinker et al. 2009). Furthermore, individual specialisation can be related to animal personality, i.e. repeatable behavioural characters such as risk-aversiveness (Coleman and Wilson 1998; Sih et al. 2004; Réale et al. 2007) or differences in learning ability (Dall et al. 2012).

Individual diet specialisation can be related to variation in individual fitness (e.g. Bolnick et al. 2003), and the degree of individual specialisation can vary between populations, creating complex ecological within-species structures (e.g. Araujo et al. 2011; Elliot Smith et al. 2015; Rosenblatt et al. 2015). Furthermore, individual specialisation often results in varying dietary overlap between individuals (Roughgarden 1972; Dalerum et al. 2012). Niche breadth characters such as individual specialisation and dietary overlap can thus determine the impact of predation on prey communities (Roughgarden 1972), but the diversity of the prey pool can hence also impact fitness in generalist predators. Especially if individuals would have rigid rather than plastic feeding strategies, i.e. exhibiting low learning rates and/or low opportunism.

To understand individual specialisation and its causation, it is important to disentangle the effect of innate preferences from the influence of lifetime experience (e.g. varying resource availability) on the development of individual strategies. At present, many studies are done on wild animals, and there is often a relationship between feeding strategy and ecological opportunity, i.e. habitat quality or food availability (e.g. Sidorovich et al. 2001; Elliot Smith et al. 2015; Rosenblatt et al. 2015). However, individual preferences could also be experimentally tested on animals bred in controlled environments. This would allow us to separate between individual specialisation and effects of prey availability, energy and nutrient content, capturing difficulty, handling time and individual preferences.

Information on individual specialisation, dietary overlap and niche breadth could be useful in translocations of endangered species (including reintroductions) to assess mortality patterns and identify and/or restore suitable habitats to facilitate survival and reproduction. Furthermore, individual variation in the ability to adapt to novel food sources, including learning time, could also affect the probability that an individual fails or copes in the release environment (Põdra et al. 2012). The level of behavioural plasticity in individuals has been linked to personality (Benus et al. 1987; Rodriguez-Prieto et al. 2010; Herborn et al. 2014), which in turn can affect survival in translocations (Bremner-Harrison et al. 2004; Haage et al. 2017). Hence, individual differences in behavioural plasticity could be one mechanism explaining mortality patterns in translocations.

To examine the occurrence of individual specialisation, we did a feeding experiment on captive bred European minks (*Mustela lutreola* (L. 1761)) in a translocation programme (see Maran et al. 2009). The European mink is a small semi-aquatic and solitary living carnivore which mainly inhabits fresh water bodies such as riverbanks, brooks and wetlands. Since the nineteenth century, the species has declined heavily, and at present, only a few isolated populations remain in the former distribution area (Maran and Henttonen 1995; Maran et al. 1998a, 1998b). It is classified as critically endangered on the red list (IUCN Red List 2015), and it is listed in Appendix II of the Bern Convention. The species is classified as an opportunistic generalist and has a fundamental niche focusing on amphibians, fish, crustaceans and mammals (Sidorovich et al. 1998; Maran et al. 1998a). In NE Europe, the diet is dominated by amphibians and fish, but crayfish (*Astacus spp.* Fabricius 1775) can also dominate when abundant (Sidorovich et al. 1998; Sidorovich 2000; Maran et al. 1998a; Põdra et al. 2012).

Although the European mink is classified as a generalist, there are indications of individual dietary specialisation. Data collected in Belarus have shown a mix of generalists and frog or crayfish specialists (Sidorovich et al. 2001), and Estonian data also indicates the existence of fish specialists (Põdra et al. 2012). Within the translocation programme, captive-bred European minks have been shown to develop a natural diet over the 60 days following release. Natural prey species were increasingly (1.5–3 times) captured, whereas atypical prey species declined fivefold over the same period (Põdra et al. 2012). The survival of released individuals have been shown to depend on personality (Haage et al. 2017), which could suggest that the time it takes for an individual to adjust to wild conditions and shift to a natural diet is affected by individual specialisation or learning time.

By using animals that are reared in a controlled environment with identical feeding routines, we examine whether or not individual specialisation is affected by innate preferences and learning. We examined individual differences in the formation of preferences and specialisation by including novel prey species and investigating learning times. The prey species included noble crayfish (*Astacus astacus* (L. 1758)), house mouse (*Mus musculus* L. 1758) and Baltic herring (*Clupea harengus membras* L. 1761). We expected individuals to have varying dietary preferences and to find a mix of generalists and specialists. Furthermore, we expected individuals to differ in learning ability. We discuss the findings in relation to conservation implications.

Methods

Housing

In Estonia, the European mink is subject to a reintroduction programme in accordance with the European mink action plan.

All released animals were bred at the off-public conservation breeding facility of Tallinn Zoological Gardens. The husbandry of the animals was designed to minimise human contact, and the animals lived in individual outdoor enclosures (200 × 400 × 180 cm) that were partially roofed. The enclosures contained tree stumps, tubes, vegetation of varying degree and water for swimming (64 × 35 × 30 cm). All enclosures had a nest-box with two compartments (each compartment being 34 × 25 × 27 cm) connected to the enclosure by a ladder. The animals were fed once a day with rat, Baltic herring, chicks, quails or minced meat mixed with carrots and vitamins.

In this study, we performed feeding experiments on animals at the breeding facility. During the experimental period, which lasted approximately 3 weeks, the European minks received food twice a day, through two cafeteria experiments. No additional food was provided, with the exception for one individual which received supplementary food (mincemeat) every day after the experimental feeding bouts due to weight loss.

Prey species

The prey species in this study included noble crayfish, house mouse and Baltic herring, hereafter referred to as crayfish, mouse and fish. However, the European minks used in the experiments had no previous experience of eating crayfish or mouse, which thus acted as mutual controls.

The crayfish were provided by a crayfish monitoring team in Estonia. The fish were distributed by Tallinn Zoological Gardens, as it was a standard food item. The mice were provided by Tallinn Technological University. Other suitable prey species were not available for logistic reasons. For ethical purposes, all prey individuals were euthanized before the start of the study. This also excludes potential effects of differences in capture time and technique. The food items were stored frozen in plastic bags and thawed before each trial.

Experiments

In order to investigate individual diet specialisation, it is recommended to sample multiple individuals over time, where the amount of time should be adapted to the study species and biological questions at hand (see Araujo et al. 2011). Here, we quantified the degree of individual diet specialisation in European mink by experimentally testing multiple captive-bred individuals ($N = 9$) over time through repeated trials ($N = 28$). We measured which prey item was consumed first and which prey item(s) were rejected, i.e. neither cached nor eaten. In addition, we compared individual learning times by investigating how readily the animals switched prey items over time. Caching behaviour is common in mustelids (e.g. Yeager 1943; Schmidt 1943; Räber 1944; Erlinge 1969), but as it is poorly understood, we chose to not include it here.

The experiments were conducted in September 2007 at the off-public conservation breeding facility of Tallinn Zoological Gardens in Estonia. The facility holds 100–120 European mink. Nine adult animals in good health, aged 1 to 4 years, were used ($N_{\text{female}} = 4$, $N_{\text{male}} = 5$). We did not consider age in this study, as age does not affect survival in reintroductions (Maran et al. 2009), and as it has no significant impact on behaviour in the form of personality (Haage et al. 2013). Furthermore, the sample size is small wherefore it is preferable to avoid additional variables (see *Statisics*). Within the test group, there were two pairs of siblings (M1 and M3; F2 and F3) and one pair of half siblings (M3 and F4) but no other close relations. The individuals were chosen based on what was logistically possible with respect to everyday management at the conservation breeding facility.

The cafeteria experiments consisted of two feeding trials per day between 08:00 AM–10:30 AM and 17:00 PM–19:30 PM. An observer (the same person in all trials) standing in the neighbouring enclosure recorded the choices made by the animal by protocol and by recording with a Sony handycam DCR-DVD 106E. The trials lasted a maximum of 10 min but were ended earlier if all prey items were cached and the individual had started to eat. All individuals participated in a total of 28 trials. The number of trials was set by our limited access to prey. In each trial, a crayfish, a mouse and a fish were presented in plastic containers (11.5 × 11.5 × 4.0 cm) placed next to each other in a random order. Each European mink had their own set of containers, and they were placed centred in the enclosures 0.7 m from the ladder to the nesting boxes, from where the animals were released at the start of each trial. The prey items were approximately the same weight in all trials, and to meet this requirement, several fish had to be used at some occasions. The amount of edible parts on the different prey species varies, however, and minks do, for example, not eat crayfish claws and often leaves the carapace as well. The amount of food given during the two daily trials covered the animals daily energy requirements with the exception for one animal that got supplementary food (see *Housing*). By the end of each trial, all prey items were left in the enclosure.

Statistics

When sample sizes are small, variable reduction is preferable in statistical testing. Here, we had only nine test individuals, but three prey items that could be either eaten or rejected, resulting in a total of six variables. To investigate if some of these variables (choices) reflected similar information, and thus whether the number of variables could be reduced, we used principal component analysis (PCA). Principal components were retrieved if they had an Eigenvalue of 1 or more, and we did not use any rotation procedure. Values over 0.4 were regarded as salient. For each component, the variables to be used in further analyses were chosen based on biological significance for the hypotheses. As could be expected, the analysis showed that the value representing rejection of each prey item was negative in relation to values representing eating the same prey item. Hence, the choice to eat or reject a prey item reflected the same information, and we therefore excluded the rejection variables. The remaining variables, which were included in further analyses, were eating mouse, fish and crayfish (Table 1).

Due to the categorical nature of the data, chi^2-tests were used to analyse differences in feeding preferences between individuals and differences in the total consumption ratios of all individuals as a group. To measure feeding preferences of the whole group over time, we used non-parametric spearman rank correlations. Changes in individual preferences over time were analysed with logistic regressions.

As the composition of the prey pool in this study was artificial, we did not use the classical measures used in studies of individual specialisation in the wild, for example, WIC/TNW (within individual component/total niche width; see Araujo et al. 2011). Calculating the total number of prey eaten to reflect the preference for each species would not be a representative, as it is not possible to assess eating preferences for a food item that has never been tasted. Hence, to classify individuals as specialists and generalists, and to take learning into account, we instead calculated the proportion of each prey species eaten after the first trial when the prey species was actually eaten (if it was ever eaten). However, if there were five or fewer trials left when a prey species was eaten for the first time, no ratios were calculated due to the low amount of data, as this would lead to an unreliable estimate. To distinguish between specialists and generalists, we followed Sidorovich et al. (2001), where individuals were considered specialists when at least 60% of their diet consisted of one prey species.

All analyses were performed with STATISTICA version 12.

Ethical consideration

The animal testing in this study did not require permission according to Estonian law and EU-legislation. Nonetheless, the deepest regard was taken to animal welfare in the experimental design. After the experiments were completed, the animals were again kept according to the ordinary routines at the breeding facility.

Results

When the food items were presented, the animals examined them briefly by sniffing and/or visual inspection before carrying one or more items to some location in the enclosure or to the nesting box. Immediately after caching food items, the animals always selected one prey item to eat. The investigator identified the prey items that the animals chose to eat visually or by hearing, as the sounds of European mink eating the different prey items were distinct.

Table 1 Principal components of the variables 'eating' and 'rejecting' different prey items in feeding trials ($N = 28$) with captive European mink ($N = 9$). The total proportion of explained variation was 61.7%, and the components are unrotated. Values of 0.400 or more were regarded as salient and are marked in italics

	Component 1	Component 2
Eat mouse	−0.021	*0.908*
Eat fish	*−0.873*	−0.110
Eat crayfish	*0.894*	−0.208
Reject mouse	0.223	*−0.426*
Reject fish	*0.648*	0.066
Reject crayfish	*−0.775*	0.086
Expl.Var	2.631	1.072
Prp.Totl	0.438	0.179

As a group, the European mink ate mouse in 2.7% of the trials, fish in 47% of the trials and crayfish in 50% of the trials. The different prey items were eaten in significantly different ratios compared to the null hypothesis ($p < 0.001$). There were also individual differences in the total amount of fish ($p = 0.002$) and crayfish ($p < 0.001$) eaten during the trials. There was no such change for mice (Table 2).

The feeding preferences of the European mink as a group changed over time, as the spearman rank correlations revealed that fish was eaten less often over time ($p = 0.007$; $R = -0.50$), whilst crayfish was eaten increasingly more often ($p < 0.001$; $R = 0.89$). Mouse consumption did not change significantly over time (Table 2).

On an individual level, the logistic regressions showed that individuals differed in their propensity and fastness to learn to eat novel prey items. Some individuals, such as M5, switched to eating crayfish within the first seven trials, whilst others, e.g. M4 and F4 switched to crayfish during the last few trials. Overall, two main patterns emerged; only increasing crayfish consumption or switching the preferred type of food from fish to crayfish. The first pattern with increased crayfish consumption was shown by individuals F1, F2, F3 and M3, whilst prey switching was shown by M4, M5 and F4. Note, however, that M2 ate significantly less fish and had a trend of eating more crayfish. One individual (M1) did not change any feeding preference over time (Fig. 1; Table 3).

Three individuals were classified as crayfish specialists (Number of individuals $[N]_{sex}$; $N_m = 2$; $N_f = 1$), two as fish specialists ($N_m = 1$; $N_f = 1$) and the remaining four as generalists ($N_m = 2$; $N_f = 2$; Table 4). Note, however, that one of the animals classified as a generalist (M3) was close to being a

Table 2 A combined result table for Chi^2-test and Spearman rank correlations on feeding preferences in captive European mink (N = 9). Section **A** shows individual differences in the ratio of different prey eaten. Df = 8 in all cases. Section **B** shows that the different prey items were eaten in different ratios by the whole group of individuals. Df = 2 in all cases. Section **C** shows the change over time (trials) in preferences for the whole group of tested individuals

		Chi^2	Spearman (R)	p
A	Mouse	12.000		0.151
	Fish	24.754		0.002
	Crayfish	30.648		<0.001
B	All prey	93.973		<0.001
C	Mouse		−0.022	0.913
	Fish		−0.500	0.007
	Crayfish		0.893	<0.001

crayfish specialist, as its proportion of crayfish was 59.3%, and the limit for specialism was set to 60%. Although the sample size was too low for statistical testing, there were no indications of sex differences.

Discussion

The general feeding pattern of captive-bred European mink showed that they preferred fish and crayfish over mice. This confirms dietary patterns found in the wild where aquatic prey comprises a larger proportion of the diet than terrestrial prey (Sidorovich et al. 1998; Maran et al. 1998a). At the individual level, however, captive-bred European mink displayed a mix of feeding strategies, which suggests that individual specialisation occurs also in a controlled rearing environment. Furthermore, although crayfish in general was consumed increasingly often over time whilst consumption of fish decreased, the rate of learning in relation to novel (but natural) prey varied between individuals. Despite the low sample size of this study, these results indicate that innate diet preferences, as well as learning ability, may affect diet choice and cause complex individual feeding patterns. Thus, individual European minks could handle ecological opportunities in prey availability in different ways, which could have consequences for how they cope with new situations.

Previous findings on wild European mink have indicated that dietary preferences vary between individuals, resulting in a mix of generalist and specialist feeding strategies within the population (Sidorovich et al. 2001; Põdra et al. 2012). This study found a similar distribution of generalists and specialists. Three animals were classified as crayfish specialists, two as fish specialists and four as generalists. However, it should be noted that the individuals classified as fish specialists (M4 and F4) started to eat crayfish during the last trials and might rather be slow learners than actual fish specialists. Although we have classified diet strategies as generalist or specialist, it is possible for individuals to display more mixed strategies. Still, the main pattern found by studying individual learning

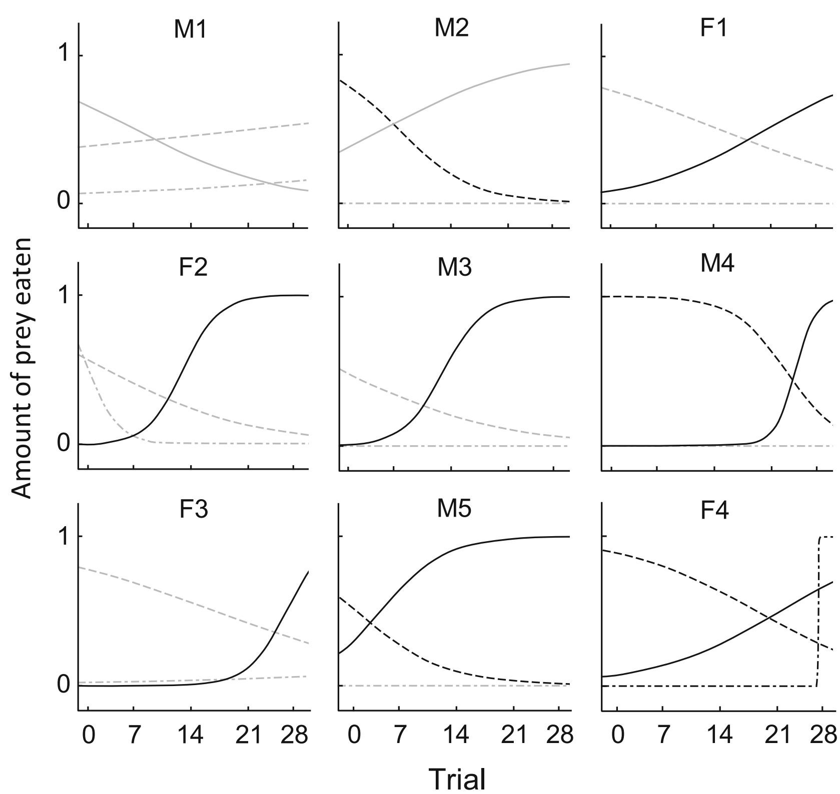

Fig. 1 The log-regression relationship between trial (N = 28) and prey items eaten by captive European mink (N = 9). *Solid lines* indicate crayfish, *evenly dashed lines* fish and *unevenly dashed lines* mouse. *Black lines* mark significance ($p \leq 0.05$) and *grey lines* mark non-significance according to logistic regressions. *F* represents females and *M* males

Table 3 *P* values and chi^2-statistics for logistic regressions on individual feeding preferences over time (trials, $N = 28$) in captive European mink ($N = 9$). 'Slope' signifies the steepest part of the slopes of the logistic curves for each individual. Empty slots represent cases where there was no positive choice during any trial. Each column represents an individual, and F stands for female and M male

		M1	M2	F1	F2	M3	M4	F3	M5	F4
Mouse	*p*	0.680			0.082			0.750		0.003
	Chi^2	0.170			3.000			0.100		8.600
	Slope	0.008			−0.110			0		6.700
Fish	*p*	0.660	0.004	0.110	0.081	0.130	<0.001	0.130	0.040	0.037
	Chi^2	0.200	8.200	2.600	3.000	2.300	11.000	2.200	4.200	4.400
	Slope	0.005	−0.049	−0.020	−0.025	−0.023	−0.070	−0.018	−0.042	−0.027
Crayfish	*p*	0.061	0.056	0.035	<0.001	<0.001	<0.001	0.0055	0.0056	0.037
	Chi^2.	3.500	3.700	4.400	22.00	21.000	14.000	7.700	7.700	4.400
	Slope	−0.025	0.027	0.028	0.100	0.090	0.170	0.095	0.057	0.029

supports that there are generalists that eat both fish and crayfish and specialist that prefer only crayfish.

Considering that our data originated from captive-bred animals which were raised on the same diet in a controlled environment, finding distinct individual feeding strategies is perhaps surprising. If individual specialisation and learning time are at least partly independent from ecological opportunity and lifetime experience, e.g. prey abundances during rearing or dispersal, it is possible that the differences could be innate and/or related to personality trait domains (groups of correlated personality traits) such as neophilia or boldness (aptitude to risk-taking).

Personality is both heritable and shaped during ontogeny (van Oers et al. 2005; Groothuis and Carere 2005). It has been shown to impact fitness (e.g. Smith and Blumstein 2008) and has also been connected to feeding choices (Bergvall et al. 2011). In the European mink, this is of interest, as the personality trait domains of boldness and exploration have been shown to impact survival of captive bred individuals after release into the wild (Haage et al. 2017) and individuals that score high on personality trait domains generally form routines quickly, whilst low-scoring individuals adapts continually to changes in the conditions (Benus et al. 1987; Rodriguez-Prieto et al. 2010; Herborn et al. 2014). After release, captive bred minks do adapt to novel natural prey items (Põdra et al. 2012), and their ability to adapt has not been seen as a matter of concern. Here, we show that they also learn to eat novel prey species in captivity. However, this study also shows that individuals differ in learning time, which perhaps could be related to their level of opportunism. The time it takes to learn to capture and eat novel prey could affect the probability of individual survival within the first weeks after translocation. Further tests could determine whether the reaction towards novel food is linked to animal personality and hence possibly reveal a mechanism explaining individual specialisation and the effect of personality on survival in European mink.

Table 4 The proportion (Prp.) of prey items eaten by captive European mink ($N = 9$) after the first trial was eaten during 28 feeding trials. If there were five or fewer trials left when an individual first ate a new prey item, the proportions were not calculated. Individuals having 60% or more of their diets comprised on one prey species were classified as specialists according to the definition of Sidorovich et al. (2001)

Individual	Prp. mouse	Prp. fish	Prp. crayfish	Feeding strategy
M1	0.111	0.560	0.346	Generalist
M2	0	0.259	0.833	Crayfish specialist
F1	0	0.538	0.476	Generalist
F2	0.040	0.304	0.842	Crayfish specialist
M3	0	0.273	0.593	Generalist
M4	0	0.815		Fish specialist
F3	0.091	0.577	0.500	Generalist
M5	0	0.160	0.852	Crayfish specialist
F4		0.630	0.500	Fish specialist

To facilitate for both slow and fast learners in reintroductions, it is important to take fundamental niche into consideration when choosing or restoring reintroduction sites. Alternatively, a wider dietary breadth could be beneficiary for generalists in captive breeding programmes involved in reintroductions. This could be applicable for the European mink, as there was a mix of feeding strategies. Furthermore, the amount of crayfish eaten increased significantly over time in seven out of nine individuals, and the remaining two showed positive trends. This indicates that crayfish is a preferred prey when available which might deserve special attention in European mink conservation efforts. The parasite-induced (*Aphanomyces astaci* Schikora, 1906) decline of the noble crayfish in Finland (see Westman 1973) has indeed been suggested as a driver of the extinction of the European mink population in Finland (Henttonen 1992). Although this has later been suggested to not be a major cause of decline (Maran and Henttonen 1995), the European mink is critically endangered, and small populations can be sensitive even to weak drivers (see Caughley 1994).

To conclude, both innate preferences and learning seem to be of importance for dietary preferences in European mink. Diverse feeding strategies, both generalists and specialists, have now been observed both in wild animals and in controlled experiments. Here, we have also shown that learning rates towards novel but natural prey items differed between individuals. This type of behavioural plasticity could potentially be of concern in conservation, as it can be related to personality, which has been shown to affect survival of reintroduced European mink.

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